Short title: ***C. cautella* in rapidly pulsed plumes**

Flight behaviour of *Cadra cautella* males in rapidly pulsed pheromone plumes.

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Abstract. Airborne pheromone plumes in wind comprise filaments of odour interspersed with gaps of clean air. When flying moths intercept a filament, they have a tendency to surge upwind momentarily, and then fly crosswind until another filament is intercepted. Thus, the moment-to-moment contact with pheromone mediates the shape of a flight track along the plume. Within some range of favourable interception rates, flight tracks become straighter and are headed more due upwind. However, as the rate of interception increases, there comes a point at which the moth should not be able to discern discreet filaments but, rather, should perceive a 'fused signal'. At the extreme, homogeneous clouds of pheromone inhibit upwind progress by representative tortricids. In a wind tunnel, *Cadra cautella* (Walker) (Lepidoptera: Pyralidae) were presented with 10 ms pulses of pheromone at a repetition rate of 5, 10, 17, and 25 s^{-1}, and a continuous, internally-turbulent plume. Pulse size and concentrations were verified with a miniature photoionization detector sampling surrogate odour, propylene, at 100 Hz. Male moths maintain upwind progress even at plumes of 25 filaments s^{-1}. Furthermore, moths exhibited greater velocities and headings more due upwind at 17 and 25 Hz than at the lower frequencies or with the continuous plume. It is hypothesized that either *C. cautella* possesses a versatile sensory system that allows the resolution of these rapidly pulsed pheromone plumes, or that this species does not require a 'flickering' signal to fly upwind.

Key words. *Cadra cautella*, turbulence, pheromone, plume, anemotaxis, attraction

Introduction

Odour molecules released into an airflow form a plume as the wind takes them from their source. Such odour-plumes are influenced by molecular and turbulent diffusion as they are carried downwind (Murlis, 1986). The effect of these forces is to create an expanding, filamentous, structure within the plume. Gaps between filaments expand as the plume travels away from its source and the diameter of the filaments also increase with distance from source (Murlis *et al.*, 2000). The effect of this is that a plume, perceived by a flying insect, would consist of a series of bursts of odour of variable strength (concentration) and spacing. An insect flying in such a plume could not orient toward a source based on comparisons of odour concentration between two sequentially contacted filaments, because the stronger signal would not necessarily be nearest the source (Murlis & Jones, 1981). Furthermore, in nature, instantaneous wind direction (estimated on contact with an odour filament) does not necessarily provide reliable information to determine direction toward the source of odour (David *et al.*, 1982; Elkinton *et al.*, 1987; Brady *et al.*, 1989). Given these constraints, a useful strategy to locate a female (*i.e.*, the source of pheromone), may be to momentarily surge upwind on contact with one filament and then zigzag crosswind to increase the likelihood of intercepting another. A consequence of the frequent misalignment of the instantaneous wind direction (estimated at contact with odour) with the direction toward the odour's source, is that flying in the instantaneous upwind direction sometimes aims the moth away from the plume and its source.

Orientation by moths to odour sources is believed to be mediated by moment-to-moment contact with filaments of the odour. If so, a moth in flight would change its course angle with interception of pheromone, directing flight more toward upwind, whereas loss of contact with the odour signal would result in a more crosswind heading (Baker, 1990; Kaissling & Kramer, 1990). The role of rate of filament encounter in anemotactic orientation to pheromone proposed for flying moths bears similarity to Kramer's (1986) model for orientation of walking silkworm moths (*Bombyx mori*) to upwind sources of pheromone. Using pulse frequencies of 0.4, 0.8, 1.7, and 3.3 Hz, upwind velocity and accuracy of heading due upwind were enhanced at the highest pulse

frequency tested. Although this finding applies to walking and not flying manoeuvres, there is a general similarity in the forms of the track taken between walking *B. mori* – fairly straight with 3.3 Hz and a zigzag at the lowest rates – and flying *C. cautella*.

Mafra-Neto & Cardé (1995b) found that *Cadra cautella* (Walker) (Lepidoptera: Pyralidae) steered more toward upwind, turned less frequently, and flew upwind more rapidly in plumes of pheromone pulsed at 5 Hz than in plumes pulsed at 0.6 Hz. *Heliothis virescens* exhibited similar reactions in plumes pulsed at 4 Hz (Vickers & Baker, 1996). However, it seems likely that the ability of a flying moth to resolve a flickering signal must diminish at a frequency that exceeds the response rate of that insect's neural circuitry. The number of action potentials produced by pheromone-sensitive sensilla of *Trichoplusia ni* was reduced by half when pulsed stimuli were separated by 30 ms (Grant *et al.*, 1997). Similarly, sensory cells of *Antheraea polyphemus* can resolve 20-ms pulses of pheromone up to 5 Hz (Rumbo & Kaissling, 1989), and those of *Manduca sexta* are capable of resolving 20 ms pulses of bombykol up to 3 Hz (Marion-Poll & Tobin, 1992). Summed potentials of responsive antennal sensory cells, recorded in electroantennograms, may not achieve the same resolution, and signals sent to the central nervous system by way of interneurones may or may not be conserved.

Moths of many species seem to respond to the frequency content of an odour signal. At one extreme, arrestment of upwind flight has been demonstrated in *Adoxyphyes orana* (Kennedy *et al.*, 1980, 1981) and *Grapholita molesta* (Willis & Baker, 1984) when moths were provided clouds of pheromone that lacked notable pockets of clean air. However, when pheromone 'clouds' were pulsed at intervals of 1 or 0.5 s^{-1}, *G. molesta* flew upwind (Baker *et al.*, 1985), evidence that signal 'flicker' is important for upwind progress. The work reported here aimed to discover the rate of flicker at which such a change in flight behaviour (*e.g.*, arrestment of upwind flight) is exhibited in *C. cautella*.

Materials and Methods

Insects

Moths were reared from eggs to last-instar larvae in 1-L jars containing rolled oats, brewer's yeast and glycerine (see Mafra-Neto & Cardé, 1995a). For experiments, last-instar larvae were removed from the colony and sexed. Males were placed in plastic holding containers (6 x 18 x 12 cm) held in an environmental growth chamber at 25 °C, 16:8 L:D and ~ 65% R.H., and allowed to pupate. Upon eclosion, adults were transferred to a 30 x 30 x 30 cm plastic screened cage and held in a growth chamber with free access to 10% sucrose. Animals tested were 2-4 days post-eclosion.

Wind tunnel

A wind tunnel was fabricated with three sheets of 3 mm clear polyacrylic (Vivac®). Each sheet was bent into a ∩-shape and connected to a 150 cm wide frame to create a symmetrical semi-cylinder 300 cm long with a maximum centre height of 150 cm. A floor was constructed with 10 mm clear Plexiglas® sheets. A push-pull airflow system was used with variable speed motors operating the upwind fan and downwind exhaust. Wind velocity in the tunnel was set at 50 cm s^{-1}. Laminar airflow through the tunnel was created by a section of aluminum honeycomb (15 cm deep x 1.5 cm diameter cell Hexel®) immediately downwind of the upwind fan. Two oblong openings cut into one side of the tunnel, 27 cm from the upwind and downwind ends, allowed access to the tunnel, and were covered with clear polyvinyl sheets so that airflow was not disturbed during flights. Both ends of the tunnel were capped with 1 mm mesh screening to prevent escape of moths. The entire tunnel was covered with white cotton sheeting to reduce visual distractions outside the tunnel.

The tunnel was housed in a room with a controlled environment of 26-28 °C and 60-70% R.H. Two banks of 25 watt clear, dark red (Philips Colortone®) and opaque white (Philips) incandescent lights were arranged on either side of the room and illuminated the ceiling. Inside the wind tunnel, light levels were adjusted to 6 - 9 lux with voltage regulators. The floor pattern

consisted of randomly placed but non-overlapping red paper dots (6 cm diameter) at a density of 60 dots m^{-2} on a white floor.

Odour sources

Odour-containing pipettes were prepared as follows. The reducing collar of a Pasteur pipette was bent to a 135° angle. Tips were cropped to 2 cm from the angle apex, resulting in a bore diameter of approximately 1.5 mm.

Synthetic pheromone components (IPO, The Netherlands) of (*Z,E*)-9,12-tetradecadienyl acetate and (*Z*)-9-tetradecenyl acetate were mixed in a 10:1 ratio and serially diluted to 10 ng μl^{-1}. A filter paper (Whatman No. 1) disk 0.7 cm in diameter was impregnated with 10 µl of synthetic pheromone solution and inserted into a pipette for immediate use in wind tunnel assays. To ensure a relatively constant level of pheromone concentration over the course of the experiments, pipettes were replaced after testing 5 males, or approximately every 20 minutes.

Pipettes containing a pheromone disk, were inserted through the floor of the wind tunnel and set upright, either singly or as a linear array of four (2 cm apart at the base), with the aperture facing upwind approximately 15 cm above the floor. The base of the pipettes were connected by polyvinyl tubing to an electronic stimulus flow controller (SFC-2, Syntech, The Netherlands), set to provide an air flow rate of 2.5 ml s^{-1}. An intermittent plume was produced with pulsing regimes of 10 ms duration pulses presented at rates of: 5, 10, 17, and 25 Hz. When visualized with $TiCl_4$, these pulses appeared as discrete packets of 'smoke' separated by clean air. We also generated a 'continuous' plume with an internally-turbulent structure at a flow rate of 2.5 ml s^{-1}.

Plume structure

To characterize the structure of each plume, measurements of the fluctuating concentration in a surrogate plume of propylene/air mixture were made with a mini-photoionization detector (miniPID; Aurora Scientific Inc., Canada). The miniPID had a sampling rate of ~ 20 ml s^{-1} through a 1 mm^2 cross-section probe. The surrogate plume was created as described above for the

pheromone plume. The miniPID was positioned along the x- (long), y- (cross), and z- (vertical) axes using a custom-made motorized, computer-controlled traverse. Vertical and horizontal cross-sections of the plumes were sampled at 100 Hz and the signal output (voltage proportional to concentration) was digitally recorded using GemAcq4 software (Gemini Enterprises, UK). Voltage outputs of the miniPID were corrected for amplifier gain. Signal characteristics were analyzed including peak and mean concentrations, and power spectral analyses of signals were made.

Assays

Moths were held singly in a 4 cm diameter cylindrical cage made of metal screening (1 mm mesh) at the downwind end of the tunnel, 18-20 cm above the floor 2 m from the odour source(s). The cage was placed on a release platform with the open end of the cylinder facing downwind. When a moth started wing fanning, the cage was rotated 180 ° to allow the moth to take off upwind. Time to fanning and take off were noted.

Flight tracks were video recorded with a CCD video camera (Sanyo VCB-3512T; shutter speed set to 1/60 s; equipped with a 6.0 mm lens) mounted above the wind tunnel to allow coverage of 1.5 m by 1.5 m area of the tunnel, and a Sony GV-A500 Hi8 video recorder.

Video and analyses:

Flight tracks were digitized at 15 frames per second (66.7 ms) using Motus® (Peak Performance Technologies Inc., USA) software. For each vector within each track, ground speed, airspeed, upwind and crosswind speeds, track, course, drift, and interturn angles were calculated (see Charlton *et al.*, 1993, for definitions of these parameters). Also, to assess more general aspects of the flight track, the length of time required for each moth to move from the downwind to the upwind end of the field of view was determined.

The flight times of male moths were compared using survivorship analyses and fitted to a Weibull distribution (with GLIM 4.0; Numerical Algorithms Group, UK), a two-parameter (mean,

shape parameter of hazard) density function that has the exponential distribution as a special case (Aitkin *et al.*, 1989). For a given set of data, the 'shape/skewness' of the Weibull distribution is primarily determined by alpha, which reflects the instantaneous likelihood that a moth will leave the field of view. By taking this approach, it was possible to obtain relatively unbiased estimates of mean flight times, which were used to select the representative tracks shown in the figures.

Vector-by-vector analyses were carried out only for track, course and drift angles and absolute values of vectors were used to calculate means of each. For parametric procedures, the mean values of ground speed, upwind speed, crosswind speed and airspeed of each track were subjected to an analysis of variance. Effects of treatment, block, period, and day were analyzed. Statistical differences were evaluated with Bonferonni's post-hoc test.

Results

Plume structure

Pulse dimensions and mean concentrations were comparable regardless of the rate at which pulses were released. Puffs from 1- and 4-pipette sources expanded as they travelled downwind (Fig. 1).

Accordingly, peak concentration within a single pulse decreased as the plume progressed downwind (Table 1). For the 4-pipette plumes, puffs from each pipette slightly overlapped. However, four peaks were observed for any horizontal cross-section, and it seemed that concentrations at overlapping sites were not excessively distorted by superimposition. On the contrary, the geometric centre of each puff from a pipette was of a higher concentration than its outer edges (Fig 2). These large peak concentrations were visible only at the geometric centre of the pulse; edges did not show large fluctuations in peak concentration.

The time averaged cross section of the continuous plume measured 500 mm downwind from the outlet was 56 x 36 mm. At this distance from the source, the miniPID recorded a signal with a regular periodicity of ~ 9 Hz (Fig. 3).

Flight tracks

Flight tracks generally were directed more toward upwind in the high-frequency pulsed plumes than at lower frequency plumes. This difference was evident in track angles (Fig. 4), in which moths most often headed more toward upwind (0°) rather than across the wind line (90°) in plumes at 25 Hz, but moths presented with plumes pulsed at 5 Hz produced flight tracks most often headed more toward across the wind line than directly upwind ($P < 0.001$). Moths travelled more due upwind in 10 Hz and continuous plumes than in plumes pulsed at 5 Hz. Moreover, flights were generally fastest (ground speed, airspeed, upwind speed) in the 17 and 25 Hz plumes than along the more slowly pulsed plumes and, apart from crosswind velocity, speeds were always lowest for 5 Hz. On average, flights at 5 Hz required more time to progress through the entire field of view than flights to the other treatments ($P < 0.001$; Fig. 5), and flights through the 10 Hz and the constant flow plumes were slower than flights through the 17 and 25 Hz plumes. These differences are shown in typical flight tracks (Fig. 6), with the moth in the 5 Hz plume spending much of the time moving crosswind and the flight to 25 Hz moving primarily upwind, with infrequent crosswind excursions. However, a few of the 5 Hz flights were very fast (< 2 s) and virtually indistinguishable from the fastest flights to 17 or 25 Hz (Fig 7).

The relationship between pulse frequency and sustained upwind flight is not clear. However, in some flights, a portion of each flight was spent outside the plume, particularly for single-pipette delivered and 5 Hz plumes. Because the quantity of puffs in the 25 Hz plume was 5 times that of the 5 Hz plume, the above differences could reflect an increased likelihood of re-contacting the plume at higher pulse frequencies. To deal with this, only the first second of each flight (the portion of the flight that had the greatest likelihood of being within the plume's boundaries) along the single-pipette plumes was assessed. (One second of flight is based on survivorship analysis of average track angle against time with the point of inflection at *c.* 1 s). Differences among treatments with respect to ground speed and track angle existed even within

the first 15 digitized frames, but these findings essentially reflected the results exhibited by the entire digitized tracks (Fig. 8).

Discussion

In the current study, parameters of *C. cautella* flight tracks, such as ground speed and track angle, were similar in plumes pulsed at 10 Hz and in continuous plumes. However, plumes pulsed at 5, 10, 17, and 25 Hz produced flight tracks in which flight parameters differed; a shorter air-gap between pulses produced straighter upwind flights.

Generally, as odour plumes progress downwind, their structure becomes more filamentous, and changes in filament frequency are concomitant with changes in peak concentration and burst length (Murlis, 1986). In these experiments, pulse duration (*i.e.* burst length) was constant, but filament frequency was varied. The expansion of pulses with distance from source corresponds to a decrease in peak concentration, but not mean concentration within a pulse, as it travelled downwind. However, flight parameters within treatments remain consistent along the flight track, regardless of changes in concentration with distance from source. This is evident in parameters measured over the entire flight track and in the abbreviated 15-frame tracks. (Note that in 15 digitized frames, or 1 s, the plume has travelled 500 mm, which essentially covers the distance from source for the range of dimensions and peak concentrations reported here.) It is concluded that, at least for the magnitude of concentrations observed here, moths are affected by pulse repetition rate rather than changes in concentration along the plume. This is in agreement with the study of Mafra-Neto & Cardé (1998) in which flight tracks of *C. cautella* were similar when the rate at which a moth intercepted pulses (*i.e.*, the realized pulse regimes) were held constant, regardless of wind speed.

Flight tracks of *C. cautella* in 5 Hz plumes exhibit mostly crosswind excursions in both large (4-pipette) and small (single pipette) plumes, suggesting that prolonged exposure to clean air (*c.* 190 ms) elicited a crosswind turn and, perhaps, the onset of casting and 'aerobatic' flight

(i.e., large loops and figure 8s). Vickers & Baker (1992) noted that male *H. virescens* must encounter a pheromone pulse within 250 ms of leaving the last pulse if it is to continue upwind flight. Similarly, *G. molesta* increases its course angle within 150 ms of losing contact with a pheromone plume (Willis & Baker, 1988), and in *A. polyphemus* after more than 300 ms (Baker & Vogt, 1988).

The differences in flight tracks between small and large 5 Hz plumes, specifically the increase in crosswind flight in small plumes, can be attributed to the moth's inability to stay within the time-average boundaries of the plume. The probability of a moth transecting a pulse was less likely when the plume had a smaller cross-sectional area, particularly at a lower pulsing rate. Males appeared to stay within the boundaries of the large plumes for a greater proportion of time, and this is especially true of males with straightened flight paths with nearly due upwind headings (for example, at 25 Hz in Fig. 7). Therefore, such males were less likely to be exposed to clean air longer than 190 ms, demonstrated by the less tortuous flights paths of moths flying along larger plumes pulsed at 5 Hz. This relationship also held for moths flying along plumes pulsed at higher frequencies in which the clean air gap was < 90 ms.

Mafra-Neto & Cardé (1994) reported that the ground speed of flying *C. cautella* males is faster, and flight track is directed more toward upwind, when presented with a pulsed or turbulent plume than a continuous ribbon-like plume. Further, males fly faster and straighter in rapidly pulsed plumes (5 Hz) than in slowly pulsed plumes (0.6 Hz). Straight flights appear to result from the suppression of an internal counterturning program, which encompasses the following elements: a cadence of pheromone pulses above a certain frequency that contacts the antennae before the male starts to counterturn, a refractory period in which pheromone or clean air has no influence on the turning program, and a pheromone concentration at some optimum such that it promotes upwind flight behaviour but not so high as to induce flight perpendicular to the wind (Mafra-Neto & Cardé, 1996). Results of the current study are similar. Males fly straighter and faster upwind in pulsed plumes than continuous plumes, and these flight characters are enhanced with increased pulse frequency in which differences are noted between plumes pulsed at 5 Hz

and 10 Hz, and between 10 Hz and >10 Hz. This is particularly true in the case of moths provided with four-pipette plumes with their larger cross-section.

The continuous plume showed some internal turbulence, owing to its release velocity of 80 cm s^{-1}, essentially introduced to the tunnel as a jet. Generally, turbulence intensity is inconstant throughout a plume and depends on a number of parameters, including distance from source. The plume issuing from a continuous source elicited flight tracks most similar to flight tracks of moths provided plumes pulsed at 10 Hz. At 500 mm downstream, the plume possessed a regular periodicity of *c.* 9 Hz, but this periodicity would not be expected closer to or further from the source (Justus et al., 2002).

Dethier (1987) suggested that plume intermittency helps to reduce sensory adaptation. There are, however, pulse rates that cannot be resolved. Marion-Poll & Tobin (1992) found receptors of *M. sexta* can follow 20 ms pulses of bombykal applied to the antennae up to 3 Hz. Likewise, sensory cells of *A. polyphemus* that are responsive to either (*E,Z*)-6,11-hexadecadienal or (*E,Z*)-4,9-tetradecadienyl acetates can resolve 20 ms pulses up to 5 Hz, but those sensitive the third pheromone component, (*E,Z*)-6,11-hexadecadienyl acetate, only up to 2 Hz (Rumbo & Kaissling, 1989). Conversely, Lemon & Getz (1997) reported that sensory neurones of the antennae of *Periplaneta americana* can resolve 50 ms pulses of a complex odour (coconut oil) up to 20 Hz.

At a more central processing level, Christensen & Hildebrand (1997) demonstrated that a small percentage of the macroglomerular complex projection neurones (MGC-PNs) of *M. sexta* could discriminate both duration and interpulse intervals of stimuli at rather moderate rates (*c.* 10 Hz). Unlike most of the MGC-PNs observed in *M. sexta*, these neurones exhibited both excitatory and inhibitory input to a 1:1 pheromone blend of (*E,Z*)-10,12-16:AL and (*E,Z*)-11,13-15:AL. Essentially, a greater inhibitory post-synaptic potential of the MGC-PN contributes to an increased ability to follow rapid pulses of pheromone; it is the opposing activity of synaptic input that allows these particular neurones to track temporal features of odour pulses. Spatial partitioning along the antenna may be a second means of gaining resolution of pulse perception and has been

reported for some species (Hösl, 1990; Heinbockel & Hildebrand, 1998) in which receptive fields of projection neurones are restricted to only a section of the flagellum.

Because these responses reported for most other species peak at rather slow pulsing regimes (< 5 Hz), it was expected that upwind flight of *C. cautella* would arrest at the higher frequencies (>10 Hz) tested. Pulses generated at a frequency of 25 Hz had an interpulse duration of 30 ms. However, a moth flying at an airspeed of 1 m s^{-1} with a rather straight flight path encounters a realized frequency much higher than the generated frequency (Baker & Vickers, 1994; Mafra-Neto & Cardé, 1998), making the clean air duration substantially less than 30 ms, the pulse duration < 10 ms, and the realized rate of interception *c.* 60 Hz. Whether a signal at this scale can be resolved by the neural processing of *C. cautella* remains to be determined. Despite evidence of physiological mechanisms (Hösl, 1990; Christensen & Hildebrand, 1997; Heinbockel & Hildebrand, 1998) that would assist *C. cautella* in resolving high-frequency encounters with pheromone, the extreme flicker rate to which *C. cautella* males were subjected may be perceived as a fused signal in the central nervous system. If so, *C. cautella* should progress upwind, even in plumes with little or no signal flicker. In fact, Justus & Cardé (2002) tested *C. cautella* and *Pectinophora gossypiella* in homogeneous clouds and found opposite responses by these two species. *Pectinophora gossypiella* does not fly upwind in such a cloud, whereas *C. cautella* does. Further, average track angles of *C. cautella* in homogeneous clouds were similar to what we report here for rapidly pulsed plumes from 4-pipette dispensers. Although we can only speculate on the physiological mechanism underpinning this navigational ability, the ability of *C. cautella* to navigate rapidly pulsed plumes is a new finding in moths that orient toward pheromone sources.

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Table 1. Peak concentration measurements of propylene plumes generated from 1 or 4 pipettes at three locations along the longitudinal axis of the wind tunnel. Concentrations given in units of miniPID output voltage.

	Peak concentration (± S.E.) Volts		
Source	x = 50 mm	x = 100 mm	x = 250 mm
1-pipette*	0.215	0.175	0.151
4-pipette**	0.209 ± 0.013	0.143 ± 0.005	0.088 ± 0.004

* peak concentration from miniPID measurement at centre of puff

** peak concentration calculated as an average of four peaks across horizontal plane

Fig. 1. Pulse sizes, measured from miniPID signals, at 50, 100, and 250 mm from source (*i.e.* x-values). Top graph is puffs generated from single-pipettes; lower graph is puffs generated from 4-pipette set up. Note in both cases that the puff expands as it travels downwind.

Fig. 2. Cross-section mean peak concentrations measured by miniPID at 100 mm from source to determine plume width of puffs generated from 4-pipette set up. Four greatest values denote centres, or near centres, of puffs from each pipette. (0.15 V $\approx$ 17 ppm).

Fig. 3. Variance power spectrum of a continuous plume issuing from a single pipette. At 500 mm downstream, a peak in turbulence intensity occurs at ~ 9 Hz. Recordings were made with a miniPID and analyzed using Fast Fourier Transformates.

Fig. 4. Flight parameters of *C. cautella* in continuous plumes or in plumes pulsed at 5, 10, 17, and 25 Hz. Open bars represent flights in 1-pipette plumes; ANOVA procedures not performed because the amount of time moth spent in plume is unknown (see text). Shaded bars from 4-pipette plumes; ANOVA for 4-pipette plumes, * $P < 0.05$; ** $P < 0.001$; *** $P < 0.0001$. Lowercase letters denote significant differences among treatments for 4-pipette plumes only; Bonferonni's post-hoc test, $P < 0.05$. Error bars represent standard errors.

Fig. 5. Probability that moth will leave field of view for all treatments with 4-pipette plumes.

Fig. 6. Average flight tracks ('average' determined with survivorship analysis) of *C. cautella* males provided 1-pipette (a) and 4-pipette plumes (b). Wind direction is from left to right; camera was set above the wind tunnel. Dots represent position of the moth every 0.067 s.

Fig. 7. Fastest flight tracks of *C. cautella* males provided 1-pipette (a) and 4-pipette plumes (b). Wind direction is from left to right; camera was set above the wind tunnel. Dots represent position of the moth every 0.067 s.

Fig. 8. Ground speed (a) and track angle (b), ± standard error, of moths provided with single-pipette plumes. Open bars are entire digitized tracks; ANOVA, $P < 0.0001$. Shaded bars are results from first 15 frames (*i.e.*, first second) of flight; ANOVA, $P < 0.0001$. Lower case letters denote significant differences among treatments for abbreviated flight tracks only; Bonferonni's post-hoc test, $P < 0.05$. Error bars represent standard errors.

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